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The effect of seedling, site, and silviculture factors on vole damage to seedling stands in Päijät-Häme, Finland, during winter 2008/09

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Thesis Abstract

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Vole damage is one of the major threats facing silviculture in Finland, particularly during winters of peak vole abundance. In this study, winter 2008/09 vole damage data were analysed from 683 seedling stand surveys (1200 ha) conducted in summer 2009 within the province of Päijät-Häme in southern Finland. Survey data were combined with site and forest management information from the Heinola Forest Management Association database. The relationships between stand-level vole damage and 14 seedling, site, and silviculture variables were then analyzed using visual analysis, Mann-Whitney U tests, and Spearman rank correlation.

In general, seedling factors were most important and site factors were least important for explaining vole damage. Seedlings were most vulnerable to vole predation during the first two years following planting, or until a height of 50 cm was reached. Additionally, all forms of site preparation (harrowing, scalping, patch-mounding, and ditching-mounding) decreased vole damage, which was particularly low in harrowing and scalping treatments. Furthermore, pine seedlings were most susceptible to vole damage, but damage to spruce seedlings was also surprisingly high compared to prior studies.

Combining these results with prior literature would suggest that silvicultural practices can minimize vole damage by the following methods: utilizing site preparation with high soil surface area disturbance, timing reforestation for the spring following vole population crashes, encouraging natural seedling recruitment in addition to planting at full density, and avoiding pine seedling monocultures. Further research should confirm tentative observations that vole damage may be lower in stands previously dominated by spruce forests, in stands where healthy natural regeneration is present, and in stands planted in the spring rather than fall.

Keywords: vole damage, forest health, seedling stand, silviculture, site preparation, site classification, *Microtus agrestis*

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Myyrätuhot taimikoissa ovat yksi suurimmista metsänuudistamisen uhista Suomessa, erityisesti niinä talvina, kun myyräkannat ovat huipussaan. Tässä tutkimuksessa analysoitiin talvella 2008/09 tapahtuneita ennätyssuuria myyrätuhoja 683 taimikkokuviolla (1200 hehtaarilla) Päijät-Hämeessä. Kenttätutkimustulokset yhdistettiin Heinolan Metsänhoitoyhdistyksen kasvupaikka- ja metsänhoitoaineistoon. Yhdistetystä aineistosta analysoitiin myyrätuhojen suhde neljääntoista taimi-, kasvupaikka- ja metsänuudistamistekijään käyttämällä graafista ja deskriptiivistä esittämistä (keskiarvo, mediaani, kvartiilit), Mann-Whitney U testejä, ja Spearmanin järjestyskorrelaatiota.

Yleensä taimitekijöillä oli suurin ja kasvupaikkatekijöillä pienin vaikutus myyrätuhoihin. Taimet olivat herkimpiä myyrätuhoille kahden ensimmäisen vuoden aikana istutuksen jälkeen tai 50 cm:n pituuteen asti. Kaikki maanmuokkausmenetelmät (äestys, laikutus, laikkumätästys, ja mätästys) vähensivät myyrätuhoja verrattuna uudistamismenetelmiin, joissa maanmuokkausta ei käytetty. Vähiten myyrätuhot olivat äestys- ja laikutusalueilla. Männyntaimikoissa myyrätuhot olivat pahimpia, vaikka kuusentaimikoissakin tuhot olivat melko suuria aikaisempiin tutkimuksiin verrattuna.

Tulokset tästä ja aikaisemmista tutkimuksista näyttäisivät osoittavan, että myyrätuhoihin voi vaikuttaa metsänuudistamismenetelmällä. Myyrätuhoja voi vähentää maanmuokkausmenetelmillä, joissa rikotun maanpinnan osuus on suuri. Istutustyöt on syytä ajoittaa myyräkannan romahduksen jälkeiseen kevääseen. Taimet on istutettava riittävän tiheään ja luonnontaimia on käytettävä täydennykseksi. Puhtaita männyntaimikoita tulee välttää. Lisätutkimuksia tarvitaan vahvistamaan seuraavat alustavat havainnot: myyrätuhot ovat pienempiä kohteissa, joissa kuusi on ollut pääpuulajina ennen uudistushakkuuta, tai taimikoissa, joissa on täydennyksenä luonnontaimia ja samaten taimikoissa, jotka on istutettu keväällä eikä syksyllä.

Keywords: myyrätuhot, metsätuhot ja torjunta, taimikko, metsänuudistus, maanmuokkaus, kasvupaikka, *Microtus agrestis*

Forward

I am sincerely grateful to a number of people who have helped make this thesis a reality. First, I wish to thank my Finnish Forest Research Institute supervisor, Dr. Otso Huitu, for arousing my interest in vole research and providing the opportunity to conduct this study. Thanks also to Jari Yli-Talonen from the Päijät-Häme Forest Management Association in Sysmä for providing the vole damage survey data used in this analysis. I also thank the friendly KYMI team (Juha Hendunen, Kirsti Honkanen, Matti Ikäheimonen, Tiina Ojansivu, and Perttu Ylisirniö) at the Heinola Forest Management Association for their hospitality and assistance while I collected data from their database. In addition, my sincere thanks are extended to Erkki and Riikka Haverinen, who supported the completion of this project in every way imaginable, and to Juha Niemi of the Liminka Forest Management Association for checking the Finnish abstract. Finally, I am indebted to my Seinäjoki University of Applied Science thesis supervisor, Dr. Tapani Tasanen, for his patience and kind advice.

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Abbreviations and Definitions

afforestation establishing a seedling stand on old agricultural fields (*peltojen metsitys* in Finnish). Compare with "reforestation."

bank vole *Myodes glareolus*, formerly *Clethrionomys glareolus* (*metsämyyrä* in Finnish).

field vole *Microtus agrestis* (*peltomyyrä* in Finnish).

FMA Forest Management Association (*Metsänhoitoyhdistys* in Finnish).

herb-rich heath *Oxalis acetosella –Vaccinium myrtillus* forest site class (*lehtomainen kangas* in Finnish. Translation according to Finnish Forest Research Institute nomenclature, Ylitalo 2010, 54).

mesic heath *Vaccinium myrtillus* forest site class (*tuore kangas* in Finnish. Also "mesic forest" in Finnish Forest Research Institute nomenclature, Ylitalo 2010, 54).

MHY Metsänhoitoyhdistys (*Forest Management Association* in English).

reforestation establishing a new seedling stand on previously forested areas following tree removal (*metsänuudistus* in Finnish). Compare with "afforestation."

site preparation mechanical soil disturbance, also known as soil preparation (*maanmuokkaus* in Finnish). Methods included in this study are harrowing (*äestys*, also known as disc-trenching), scalping (*laikutus*), patch-mounding (*laikkumätästys*), and ditching-mounding ([*ojitus*]*mätästys*).

sph stems per hectare, a measurement of tree or seedling density.

stand a continuous area of forest with similar age, species composition, etc. throughout and delineated from the surrounding forest for the purpose of forest mapping and management. Also known as compartment, stand compartment or forest cover polygon (*kuvio* in Finnish).

tundra vole *Microtus oeconomus* (*lapinmyyrä* in Finnish)

water vole *Arvicola terrestris* (*vesimyyrä* in Finnish).

1 INTRODUCTION

1.1 Overview

Finnish forest regeneration has undergone a dramatic change over the past approximately half century as reliance on natural seeding has been largely replaced with intensive artificial planting practices (Valtanen 1998, 1). As silvicultural practices intensify, so does the concern for seedling survival and vigour (Teivainen 1979, 4). The concerted effort to minimize seedling damage has resulted in extensive research to predict and reduce damaging agents. A particularly striking example of this is the globally intensified focus on vole-induced seedling damage (recent examples include Canada: Sullivan & Sullivan 2001a; Sullivan, Sullivan & Hogue 2001b; United States: Cadenasso & Pickett 2000; Witmer, Snow, Humberg & Salmon 2009; Germany: Walther, Fülling, Malevez & Pelz 2008; Finland: Hytönen & Jylhä 2005; Huitu et al. 2009; Puukila 2010; Sweden: Hansson 2002; and multinational perspectives in Singleton, Belmain, Brown & Hardy 2010).

According to Huitu et al. (2009, 1222), voles can be regarded as one of the most serious pests facing silviculture in Northern Europe. Vole damage is widespread throughout Finland, and the tendency of voles to concentrate in small areas can cause particularly significant damage at local scales (Heliövaara 2008, 224). Voles not only cause direct seedling mortality by chewing or severing seedling stems, but also non-lethal damage to seedling stems and leaders can cause subsequent growth deformities or invasion by stem-rot fungi which reduce the value of later timber harvests (Henttonen 2001, 285-288). Indeed, it is estimated that the financial impact of vole damage in Finland during the winter of 2005/06 alone is at least 2.2-4.0 million euros, although this is likely a very conservative estimate when considering lost value of future harvests (Huitu et al. 2009). Similarly, vole damage during winter 2008/09 left at least 18 000 ha of seedling stands in southern Finland below required stocking limits (Myyrät ja pistiäiset riesana 2009), and compensations paid by insurance companies and associations in 2009 for rodent damage was over 7 million euros, or 70% of all forest damage compensations paid in that year (Ylitalo 2010, 119).

Such a large-scale problem requires a large-scale solution. Much prior research has focused on one or a few factors that influence vole damage or feeding behaviour, but there is an urgent need to approach vole damage research from the broad operational level at which silvicultural decisions are made. In this study, I take a more holistic approach by examining vole damage in relation to a wide range of site, seedling, and silviculture factors in the Päijät-Häme province of Finland. By examining which variables are most strongly linked to vole damage and relating these findings to prior studies, I propose how key site, seedling, and/or forest management variables can be selected or manipulated to minimize costly vole damage.

1.2 Background

1.2.1 Brief description of vole damage to silviculture in Finland

Vole abundance is cyclical with peaks generally occurring every 3-5 years (review in Korpimäki, Brown, Jacob & Pech 2004, 1072); in southern Finland, 3 years is considered the normal period between vole cycles (Palokallio 2011b). Damage to forest seedlings is generally greatest during vole population peaks or in the following winter when the population has begun to crash (Henttonen 2001, 285). In general, seedling damage occurs during winter months, when voles' preferred food sources (herbaceous shrubs and grasses) become scarce and voles turn to less nutritious seedlings for food (Huitu, Koivula, Korpimäki, Klemola & Norrdahl 2003; Väkevä, Henttonen & Kankaanhuhta 2010; Palokallio 2011a quoting researcher Otso Huitu). However, winter damage only becomes evident the following spring, when snowmelt reveals the damaged and killed seedlings (Palokallio 2011a quoting researcher Otso Huitu). Although winter damage is recognized as the norm for coniferous seedlings in reforestation areas, birch may be at risk in afforested fields during summer months as well (Henttonen 2001, 285; Väkevä et al. 2010).

Vole damage takes a variety of forms depending on the vole species or species group in question. In general, the water vole (*vesimyyrä*, *Arvicola terrestris*) damages seedlings by debarking the roots. Conversely, the bank vole (*metsämyyrä*, *Myodes glareolus*, formerly *Clethrionomys glareolus*) debarks or removes the seedling or sapling leader, often resulting in forked leaders ("schoolmarms") leading to stem deformities. In northern Finland, the tundra vole (*lapinmyyrä*, *Microtus oeconomus*) is a noteworthy source of both root and stem damage to seedlings. By far the most widespread damage is caused by the field vole (*peltomyyrä, Microtus agrestis*), which chews bark from around the seedling stem or severs small stems completely. (Teivainen 1979 and sources therein; Henttonen 2001; Palokallio 2011b) In this thesis, most of the damage is assumed to be caused by the field vole, and management suggestions relate primarily to this species.

The effects of vole feeding on forest seedlings exceed the immediately apparent seedling mortality (Henttonen 2001, 285). Birch seedlings which survive partial stem girldling are nonetheless susceptible to reduced vigour through a) suckering (the profusion of new shoots from the base of a deciduous stem, often following stem damage and potentially resulting in over-density and poor stem quality in suckered shoots), b) weakened stems which break years later under the weight of increased crown growth, and c) infection by stem-rot fungi, reducing both stem strength and wood quality (Henttonen 2001, 285–286). Similarly, although visible pine stem deformities caused by vole damage may gradually disappear from sight as the tree grows, the stem defect remains within the lumber during the entire life of the tree (Henttonen 2001, 288). Furthermore, studies show that seedlings weakened by previous vole damage are more susceptible than healthy seedlings to subsequent vole attack (Rousi 1983, 8).

Recent changes have been observed in vole population fluctuations (Henttonen 2001, 284; Huitu et al. 2009, 1223), and it appears that vole damage may have increased during the past decades (Heliövaara 2008, 224). Indeed, vole damage during the winter of 2008/09 was the highest ever recorded in Finland (Myyrät ja pistiäiset riesana 2009). The increase in vole damage and abundance may be due in part to increased afforestation of fields and increased nitrogen fertilization leading to abundant grass growth (Heliövaara 2008, 224). Given the high economic impact of vole damage both to individual land owners and state support systems (e.g. Kemera funding), it is important to identify and control factors affecting vole damage.

1.2.2 Factors affecting vole-induced seedling mortality

Numerous factors have been linked to the occurrence and severity of vole damage. These can be summarized by internal factors (inherent to vole population dynamics and interactions between vole species) and external factors (seedling, habitat, forest management, or environmental impacts), although there is clearly an interaction between these two. This study focuses on seedling, site, and forest management characteristics (external factors) as the variables that forest managers can more easily select and/or manipulate. Nonetheless, it is also necessary to have a basic understanding of vole population dynamics.

Population dynamics. As previously mentioned, vole damage is linked to vole population cycles, although the extent of vole damage may vary locally. Causes for this cyclic behaviour have long been researched and have been linked to predation (review in Hanski, Henttonen, Korpimäki, Oksanen & Turchin 2001), density-dependent limitations to winter food supply (Huitu et al. 2003), and intrinsic breeding behaviour during the population expansion phase (Löfgren 1989, Abstract). Spatially-correlated weather events may also play an important role in synchronizing cyclic vole populations (Huitu, Laaksonen, Klemola & Korpimäki 2008). In reality, all of the above-mentioned factors likely affect vole population dynamics, but at varying scales and at different stages in the population cycle (review in Korpimäki et al. 2004). While the debate continues on the factors driving population cyclicity, there is evidence that fluctuating vole population levels and seedling damage levels are related (Huitu et al. 2009).

Habitat and vegetation cover. Habitat characteristics also affect vole abundance and the damage inflicted on seedlings. Presence of the field vole (a habitat specialist) is linked to open grassy areas, and vole damage in forest regeneration areas is generally higher in grassy parts of the opening (Larsson & Hansson 1986 and Hansson 1994 cited in Hansson 2002, 28). Grasses provide field voles with an important food source, nesting environment, and shelter from predators. Not surprisingly, much higher damage levels have been observed on afforested fields than in forest regeneration areas (Teivainen 1979, 7). In forested environments, Hansson (2002, 31) found that vole bark consumption on deciduous trees and bushes was positively related to reforestation surface area and negatively related to seedling height, thus supporting the general assumption that fields and young, grassy forest openings provide high-risk areas for seedlings. Vegetation control through mechanical site preparation (*maanmuokkaus*), chemical herbicide application (*kemikallinen heinätorjunta*), or even boot screefing (*heiniminen*) are important not only for decreasing suitable vole habitat, but also for decreasing vegetative competition and improving light and growing conditions for seedlings. Therefore, weed control is important for the survival and growth of spruce (Hytönen & Jylhä 2008) and birch (Hytönen & Jylhä 2005) seedlings planted on former agricultural land. Habitat connectivity may also be an important factor for field voles (Hansson 2002, 32).

Snowpack conditions. As previously stated, voles consume seedlings primarily during winter, when more nutritious herbaceous food sources become scarce. When conditions under the snow are favourable for vole mobility, voles are able to access more desirable food sources and seedling damage may be minimal, whereas unfavourable conditions under the snow result in abundant vole damage (Henttonen 2001, 285). As stated by Henttonen (2001, 285), it is often said that damage is more abundant in snowy winters, but snow quality is also an important factor: vole mobility is affected by whether the snow is low-density snow formed under cold conditions, or whether it is crusty snow affected by intermittent rainfall and tightly packed to the ground.

Seedling characteristics. Vole damage is known to vary depending on seedling species and size. Both pine and birch have shown higher levels of vole damage than spruce (Teivainen 1979, 7–10; Seppänen 2010, 24), although other factors such as habitat (field *versus* forest) also influence seedling species damage differences (Teivainen 1979, 10). Vole damage risk diminishes as seedling size increases, and by the time basal diameter has reached 4 cm, birch seedlings are no longer at high risk (Väkevä et al. 2010).

1.2.3 The need for silvicultural methods of limiting vole damage

Recent studies have highlighted the inherent difficulty in predicting the location and severity of vole damage in any given year or location, due in part to a) changes in vole cycle amplitude (Huitu et al. 2009, 1223) and synchronization (Henttonen 2001, 284–285), b) possible interspecific interactions between vole species (Hansson 2002), and c) strong regional differences in vole abundance (Teivainen 1979). Additionally, climate change trends may lead to increasing frequency of severe weather events, deviations in the spatial correlation of weather events, and changes in the snowpack, which may increase the unpredictability of vole abundance and cyclicity. Difficulty in predicting cycles and understanding the factors driving such cycles underscores the importance of consistently practicing low-risk forest management. Therefore, this study examines the relationship between vole damage and specific seedling factors, site characteristics, and forest management procedures in an attempt to encourage safe silviculture practices.

Abundant research has been conducted on methods to reduce vole damage. For example, control by voles' natural predator, the Eurasian pygmy owl (*varpuspöllö*, *Glaucidium passerinum*), has been studied but shown ineffective for controlling vole damage, at least on large scales and at high vole population densities (Henttonen 2001, 288; Puukila 2010). Vole poisons have also been examined, but their effectiveness is strongly species-specific: for water voles, poisons may be the only effective reduction method, but for the widespread field vole, poison may be of little effect, particularly in afforestation areas (Henttonen 2001, 288). Repellents (non-poisonous substances applied directly to seedlings and relying on undesirable taste and smell to deter voles, Väkevä et al. 2010) and diversionary foods (foods that are more palatable than tree bark but not highly nutritious, Sullivan et al. 2001b, 104) are yet another attempt to minimize vole damage. Sullivan et al. (2001b) found that diversionary foods did reduce forest seedling damage, although the results were not significant and there was no apparent impact on mean vole population abundance. The effectiveness of repellents also varies depending on weather conditions, and they must be applied twice a year (Henttonen 2001, 288). Much more promising is the use of seedling guards (*taimisuojat*): indeed, seedling guards, together with site preparation and chemical weed control, are basic essentials for afforestation (Henttonen 2001, 286).

Poisons, repellents, diversionary foods, and seedling guards may be useful means of reducing vole damage, but they provide quite an intensive, small-scale solution. Furthermore, they provide external deterrents but do not impact the habitat suitability of the seedling stand to voles, nor do they affect the actual seedling attributes (size, species, etc.) in a way that deters vole browsing. In contrast, habitat control can be accomplished through vegetation control (through site preparation and chemical weed control, for example) or by site selection for forest types less suitable to voles. Additionally, seedling desirability can be affected by selecting seedling species less palatable to voles, and by larger seedling size. These methods of controlling vole damage through seedling, site, and forest management decisions provide a more holistic and large-scale alternative to vole management.

1.3 Research aims

This study was conducted to identify the site, seedling, and silviculture factors most strongly linked with vole damage in the Päijät-Häme province of Finland, in order to suggest means for controlling these factors and thereby limit vole damage. In particular, the following hypotheses are examined:

- Smaller, younger seedlings will be more susceptible to vole damage;
- Pine and birch will have higher damage than spruce seedlings;
- Areas with healthy naturally regenerated seedlings will have lower planted seedling mortality; and

- Factors discouraging grassiness (i.e. site preparation, minimal delay between site preparation and planting, smaller opening area, less productive sites, and pre-harvest conifer-leading forest) will also be linked with lower vole damage.

This study also includes the examination of relationships between vole damage and several additional factors (seedling density, soil type, and pre-harvest forest age) available in the data but for which no hypothesis existed based on prior studies.

All hypotheses and other observations are investigated by combining summer 2009 field survey data on seedling characteristics and vole damage with site and silviculture information from the Heinola Forest Management Association (FMA) database. The relationships between vole damage and seedling, site, and silviculture factors are then assessed using Spearman rank correlation, Mann-Whitney U tests, and visual graphics. These results are compared with prior literature, and overall conclusions are applied to practical forest management recommendations.

This study has been conducted as an independent research project, funded in part by Metsämiesten Säätiö (recipient Dr. Otso Huitu), under the broader research objectives of Finnish Forest Research Institute Project 3505, “Rodent Research” (Metsäntutkimuslaitoksen hanke 3505, “Myyrätuhotutkimus”).

2 MATERIALS AND METHODS

Thesis data were prepared in three distinct stages: field data collection in summer 2009, data compilation and extraction in fall 2009, and data summarization and analysis in fall 2010–spring 2011.

2.1 Field surveys, summer 2009

Study sites were located within the province of Päijät-Häme (Figure 1). Field measurements were completed during spring and summer 2009 by approximately 15 trainees working for the Päijät-Häme Forest Management Association. Each trainee was instructed to survey the designated stands uniformly with a sample

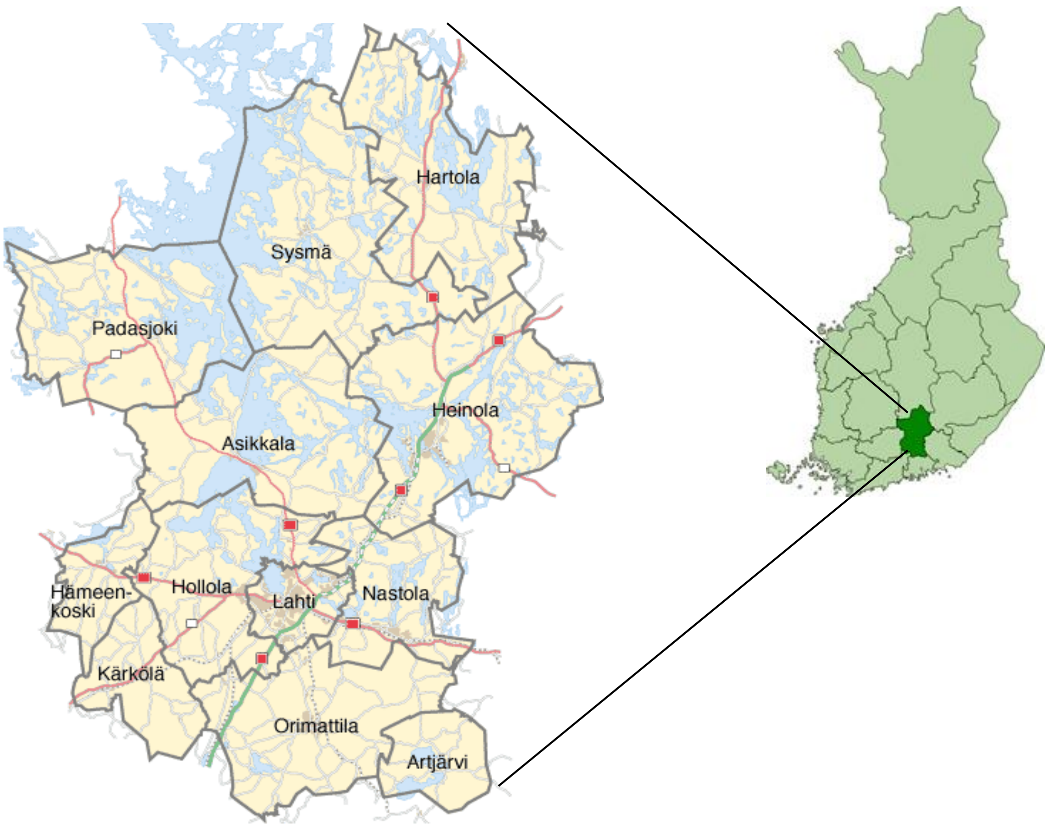

Figure 1. *Vole damage inventory areas within Päijät-Häme included Sysmä, Asikkala, Padasjoki, Heinola, Hartola, Nastola, Kärkölä, Hollola, and Hämeenkoski in descending order of area sampled. Total area surveyed exceeded 3000 ha, of which approximately 45% required fill-planting or re-planting following record high vole damages during winter 2008/09. In this thesis, a portion of the data (1200 ha) was selected for further analysis (details in Appendix 1). (Päijat-Häme map 2009; Finland map 2010)*

plot density of approximately 10 plots per stand (in practice, the amount varied widely depending on stand size). Sample plots were circular and generally 3.99 metres in radius, complying with standard forestry survey procedures. (Ohje myyrätuhoinventointiin 2009)

Within each sample plot, surveyors recorded a) average seedling height, b) the number of planted and/or naturally regenerated healthy (*kasvatuskelpoinen*) seedlings, and c) the number of planted vole-damaged/killed (*kasvatuskelvoton/ kuollut*) seedlings. To be counted, planted seedling species must be either spruce (*Picea abies*), pine (*Pinus sylvestris*), or birch (*Betula pendula*), with the added condition that the species must be suitable to the site. In addition to these requirements, naturally regenerated seedlings must be well-spaced (at least 50 cm between seedlings) and 0.5–1.5 times the height of planted seedlings. A seedling was classified as vole-damaged/killed if bark had been stripped from more than 50% of the circumference. Seedlings chewed along the leader but retaining the most recent year's growth were considered healthy. (Ohje myyrätuhoinventointiin 2009)

Sample plots must be located in areas capable of seedling growth, and surveyors were instructed to adjust the position of sample plots falling on rocky, swampy, or otherwise unsuitable areas. Additionally, surveyors were instructed not to establish sample plots in uniform, fully stocked stands (i.e. stands satisfying healthy seedling density objectives throughout). Furthermore, regeneration in naturally regenerated or seeded stands must have been established and at full density prior to possible vole damage. For pine, this equated to 2000 sph in naturally regenerated areas and 3000 sph in seeded areas; seedling density limits for spruce and birch were 1800 sph and 1600 sph, respectively. (Ohje myyrätuhoinventointiin 2009)

2.2 Data compilation and extraction, fall 2009

After the completion of summer vole-damage assessments, survey results were obtained in paper and/or electronic format from the Päijät-Häme FMA office. During November–mid-December 2009, I sorted and compiled these field data into a single electronic Excel database at the Finnish Forest Research Institute, Suonenjoki unit, under Dr. Otso Huitu's supervision. I then expanded the survey data file to include stand, site, and silviculture information, which I extracted from the Päijät-Häme FMA database in Heinola. These additional data were obtained for a portion of the total survey dataset, giving preference to survey stands with a) high quality/complete field data, b) a clear site-plan number to facilitate data matching with the FMA database, and c) forest management data as specific and complete as possible. In many cases, FMA database information included only a portion of the desired information, or information was generalized for a group of stands.

2.3 Data summary and analysis, fall 2010–spring 2011

Quality control. Given the size, complexity, and non-uniformity of the dataset, an extensive amount of time was spent cleaning and organizing the data prior to analysis. For the purposes of this thesis, the most reliable data records (representing approximately 1200 ha, or 65% of the sample plots in the composite database) were selected for further analysis. Selection criteria included a) mortality clearly linked to vole damage during 2008-2009 and meeting the requirements for mortality as outlined in sampling instructions; b) distinction by field observer of seedling species (spruce, pine, birch) and origin (natural, planted); and c) sufficient seedling density and height to allow sampling in 2009, thus eliminating extremely rocky or recently seeded sites. Furthermore, machine-planted stands, stands planted to any species other than pine, spruce, and/or birch[1], and stand summaries without accompanying sample-plot data were eliminated from final analysis. Due to poor data quality and/or quantity, the entire municipalities of Nastola and Hartola were removed. A municipality-level summary of percentage original data retained, number of stands analysed, and mean percentage of vole damage is located in Appendix 1.

[1] A slight exception would be one stand included in this analysis which, according to the Forest Management Association database, had 100 larch seedlings planted (total stand area was 4.9 ha). However, as no larch was recorded in the sampled areas and nor was there any comment about larch by the survey observer, it was assumed that the seedlings were planted on a tiny corner of the stand and therefore not included in sampled areas.

Stand summaries. For the resulting subset of data, the first step in data analysis involved converting all sample-point seedling counts to per-hectare results based on the following formula:

$$\mathrm{sph} = \frac{(\text{number of seedlings}) * 10\,000\mathrm{m}^2}{\pi \mathrm{r}^2} \qquad (1)$$

where	sph	is	number of seedlings per hectare
	π	is	pi (3.14159)
	r^2	is	sample-plot radius (in metres)

Next, each of the 683 stands (*kuviot*) was assigned a unique identification number to facilitate stand-level data summary in Excel.[2] Per-hectare stand means were then obtained by summing sample-plot values and dividing by the number of sample plots per stand for the following variables: number of healthy planted pine, spruce, and birch seedlings; number of healthy, naturally regenerated pine, spruce, and birch seedlings; number of vole-damaged/killed planted seedlings; and total number of seedlings (i.e. healthy planted + healthy natural + vole-damaged/killed planted). Mean percentage of vole-damaged/killed seedlings per stand was calculated using the following formula:

$$\%\ \text{damage/stand} = \frac{\sum(\text{plot damaged sph}) * 100\%}{\sum(\text{plot total sph})} \qquad (2)$$

where	$\sum$	is	sum of sample plot values
	sph	is	number of seedlings per hectare

This method of obtaining mean damage percentage from summed stand data, rather than a mean of individual sample-plot damage, eliminated the difficulty of dividing by zeros in sample plots with no seedlings. All further data analysis involved stand summaries rather than sample-plot level data. A complete

[2] Most often individual stands were surveyed, numbered, and analysed as a single, complete unit. However, in cases where *several* stands were simultaneously surveyed as a single stand cluster, these were assigned a single stand identification number and analysed as a single unit. In cases where a stand was *divided* into two or more distinct survey areas, each sub-stand was assigned an individual stand identification number. *In this report, analysis was conducted at the stand level, where "stand" refers to the stand, stand cluster, or stand portion having a unique stand identification number.*

description of field and forest-management data variables at the stand level is contained in Appendix 2.

Data distribution. To facilitate further analysis, the primary dependent variable—percentage of vole-damaged/killed planted seedlings per stand—was visually checked for normal distribution using a histogram (Figure 2). The assumptions of normal continuous distribution were not met because a) the damage variable is based on discrete seedling counts and is therefore non-interval data; and b) the distribution is strongly skewed to the right unlike a bell-shaped normal distribution curve. Given the non-normal distribution of the data and the limited data analysis functions available in Microsoft Office Excel 2010, results were assessed by graphing descriptive statistic parameters and conducting basic non-parametric analysis.

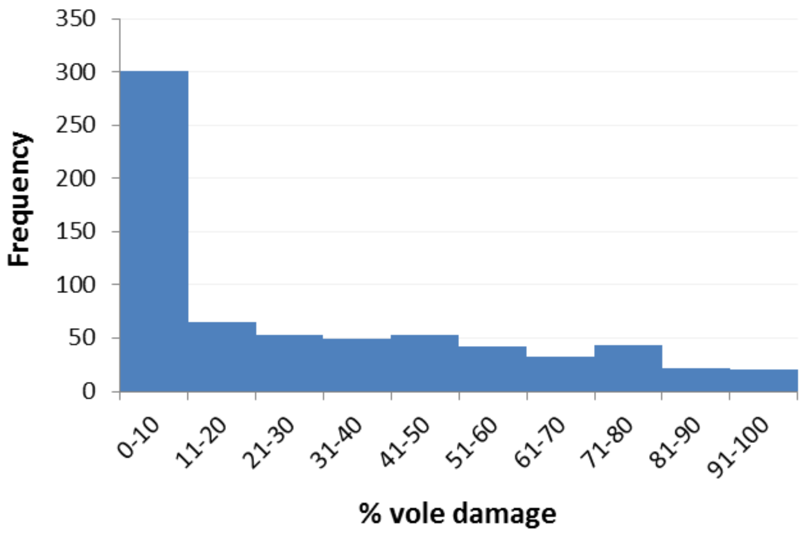

Figure 2. *Frequency distribution (histogram) illustrating number of stands within each vole damage category. Mean stand-level vole damage is defined as the percentage of planted seedlings severely damage or killed by voles in Päijät-Häme during winter 2008/09.*

Categorical analysis. For categorical independent variables (seedling size, seedling species, seedling origin, site and soil classification, pre-harvest tree species, site preparation method, and planting season), the dependent variable (percentage of vole-damage/-killed seedlings) was characterized by descriptive statistics (mean, median, first and third quartiles, and sample size). Mean and median are measures of central tendency, while first and third quartiles[3] are measures of data variance. These variables were generated using mean/*keskiarvo*, median/*mediaani*, percentile/*prosenttipiste*(0.25,0.75), and count/*laske* formulae in Excel. In graphical presentation, error bars about the median represent quartiles rather than standard deviation, standard error, or 95% confidence intervals; this was done because the latter measures of variance assume the data to be parametric (continuous variable with normal distribution), while quartiles are more suitable for assessing non-parametric data. Visually, a longer upper error bar represents right-skewed data, whereas a longer lower error bar represents left-skewed data.

In addition to visual graphics, variables with only two categories [i.e. presence/absence of healthy natural regeneration, mesic/herb-rich heath (*tuore/lehtomainen kangas*), and spring/fall planting season] were tested for significant difference by ranking the data and conducting Mann-Whitney U tests in Excel. Because Excel does not include a Mann-Whitney U test function, this was completed manually following the example in Wilson (2010). First, ranks were assigned to the vole damage data in ascending order, using the formula for averaging tied ranks [Excel formula *ARVON.MUKAAN.KESKIARVO* (datarange,1)]. These vole damage ranks were then grouped into the two relevant categories (e.g. mesic heath, herb-rich heath), and the U value was calculated for each category according to the formulae:

$$U_1 = n_1 n_2 + \frac{n_1(n_1+1)}{2} - R_1 \qquad (3.a)$$

$$U_2 = n_1 n_2 + \frac{n_2(n_2+1)}{2} - R_2 \qquad (3.b)$$

where	U_1	is	variable 1 Mann-Whitney U test statistic
	U_2	is	variable 2 Mann-Whitney U test statistic
	n_1	is	variable 1 sample size
	n_2	is	variable 2 sample size
	R_1	is	variable 1 sum of ranks
	R_2	is	variable 2 sum of ranks

[3] When data is arranged in ascending order from lowest to greatest value, the first quartile is defined as the value below which 25% of the data are located, whereas the third quartile is defined as the value below which 75% of the data are located.

Because of large sample sizes ($n_i > 20$), the significance of the U statistic was found using the normal approximation formulae to calculate z_U (Table A5.07, Alamo Colleges 2011):

$$z_U = \frac{\left|U_{stat} - \left(\frac{n_1 n_2}{2}\right)\right|}{\sqrt{\frac{n_1 n_2 (n_1 + n_2 + 1)}{12}}} \quad (4)$$

where	z_U	is	normal probability test statistic for U
	U_{stat}	is	the lesser value of U_1 and U_2
	n_1	is	variable 1 sample size
	n_2	is	variable 2 sample size

Finally, the result was checked for significance by comparing the calculated z_U with the critical z_{crit} value obtained from a z normal probability distribution table [z_{crit} = 1.65 for one-sided test (α = 0.05), z_{crit} = 1.96 for two-sided test (α = 0.025)]. The standard z_U formula used here assumes that there are not many values assigned the same rank (i.e. "ties"). The validity of this assumption is questionable in this dataset, where many ties existed particularly for 0% vole damage.

Non-categorical analysis. For comparing vole damage with non-categorical data (i.e. seedling density, stand age, stand surface area, and number of days between site preparation and planting), visual scatter plots were created and non-parametric correlation was conducted in Excel. According to standard procedures, Spearman's rho (non-parametric correlation) was calculated by ranking the data and calculating the Pearson correlation coefficient on the ranks [Excel formula PEARSON(x-variable data range, y-variable data range)], using the formula for ties:

$$r_s = \frac{\sum(x - \bar{x})(y - \bar{y})}{\sqrt{\sum(x - \bar{x})^2 \sum(y - \bar{y})^2}} \quad (5)$$

where	r_s	is	Spearman's correlation coefficient
	x	is	variable 1 rank value
	$\bar{x}$	is	variable 1 mean rank
	y	is	variable 2 rank value
	$\bar{y}$	is	variable 2 mean rank

To check for significance of the relationship, the t-statistic was used, according to recommended procedures for sample sizes greater than ten (Optional Topic—Spearman Rank Correlation Coefficient, no date):

$$t_{stat} = r_s \sqrt{\frac{n-2}{1-r_s^2}} \quad (6)$$

where	t_{stat}	is	t-statistic
	r_s	is	Spearman's correlation coefficient
	n	is	sample size

The t-statistic was compared with the two-sided t-critical value for $\alpha = 0.05$ [Excel formula *T.KÄÄNT.2S*(0.05, degrees of freedom)], and results were concluded significant only if the absolute value of the t-statistic exceeded the absolute value of t-critical. A pre-programmed Spearman rank correlation calculation Excel spreadsheet available online (McDonald 2009) was also used to check values obtained by the above method. In all cases, Spearman rank coefficients were the same those calculated by the method shown. However, this spreadsheet apparently uses an F-test rather than t-test to check for probability, and in one case (surveyed seedling density) this F-test method resulted in a significant relationship when the t-test method was non-significant.

Analysis precautions. While these basic analyses clearly and simply presents the main findings, a follow-up study could transform the data (e.g. Box-Cox transformation, Osborne 2010) and strengthen these visual results using more advanced analysis software (e.g. SAS or SPSS data analysis programmes). Such software would also enable an analysis of the interaction between factors. Additionally, a more complex formula could be employed in z_U calculation (Mann-Whitney U test procedure) to address tied rank data (Shier 2004). Finally, variables with three or more categories could be tested for statistical difference using the Kruskal-Wallis procedure (not included in Excel).

3 RESULTS & DISCUSSION

3.1 Vole damage as a function of seedling factors

Summary: Seedling factors are most important in explaining vole damage. In particular, highest damage was recorded among smaller/younger seedlings and pine seedlings. Additionally, it appears that when healthy natural regeneration was present, voles may have preferentially browsed on planted rather than natural seedlings.

3.1.1 Seedling size

Vole feeding appears to be negatively related to seedling size and time since planting (Figures 3.a and 3.b). Mean damage exceeded 45% for seedlings up to 25 cm tall, but was nearly non-existent for seedlings taller than 1 m (Figure 3.a). Similarly, damage rates for seedlings planted in 2006 were only one-third as great as for seedlings planted in 2008 (Figure 3.b). This relationship appears consistent across all measures (mean, third quartile, median, and first quartile).

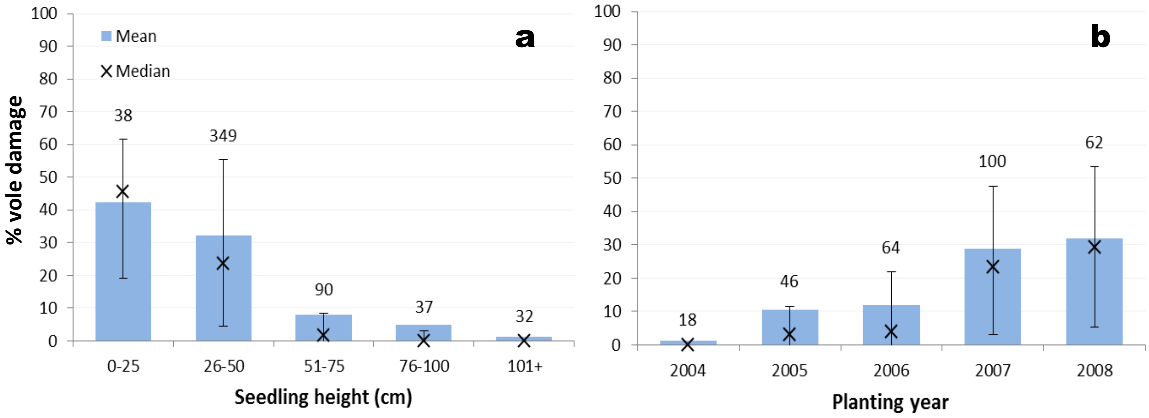

Figure 3. *Winter 2008/09 vole damage to planted seedlings in Päijät-Häme surveyed in summer 2009. Mean damage (filled bars) categorized by a) height (cm) of dominant seedling species and b) year of planting. Upper and lower error bars represent the third and first quartiles, respectively, about the median value (x), while numbers above the bars indicate sample size (number of surveyed stands).*

Due to differences in summer 2009 survey dates resulting in a possible effect of current-year (i.e. 2009) grown on height, I also checked the relationship only for stands (n=223) measured prior to June 1, but the trend was the same as for the complete dataset. (Note that vole damage in these and all other figures refers only to damage occurring during winter 2008/09.)

The inverse relationship between seedling size and vole damage is consistent with the hypothesis and with prior literature. From a spring 2009 seedling survey of vole, moose, and weevil damages near Huittinen (southwestern Finland), Seppänen (2010, 24–25) records 24% higher seedling mortality for seedlings planted in 2007 versus 2008. Seppänen (2010, 38) attributes these findings partly to the peak vole abundance in 2008, and partly to younger seedlings being smaller and weaker. In a nation-wide survey of vole damage during 1973–76, Teivainen (1979) also found a clear preference for younger seedlings. Ninety percent of seedling damage had occurred before three years from planting for birch, four years for pine, and five years for spruce; in terms of height, this corresponded to 125 cm for birch, 75 cm for pine, and 100 cm for spruce (Teivianen 1979, 7, 10). Similarly, Hansson (2002, 31) reports a negative relationship between seedling height (approximately corresponding to reforestation age) and the occurrence of vole damage on the bark of deciduous trees and bushes in 1998–99. Hytänen and Jylhä (2005, 373–374) also note vole selection for the smallest birch seedlings, although the relationship between seedling height and vole damage weakened over time as seedling height increased. Indeed, birch plantations are susceptible to vole damages only during early growth stages; once basal diameter exceeds four centimetres, vole damage is usually no longer a serious threat (Raulo 1978, 22).

3.1.2 Seedling species

Vole damage was greatest for pine (mean 35%, median 42%, n = 22), intermediate for spruce (mean 29%, median 19%, n = 587), and lowest for birch (mean 12%, median 0%, n = 36) (Figure 4). Damage levels in multi-species seedlings stands (defined as stands in which the primary species accounts for no more than 75% of the healthy pine, spruce, and/or birch seedlings; n = 38) were similar to stands dominated by birch only (Figure 4).

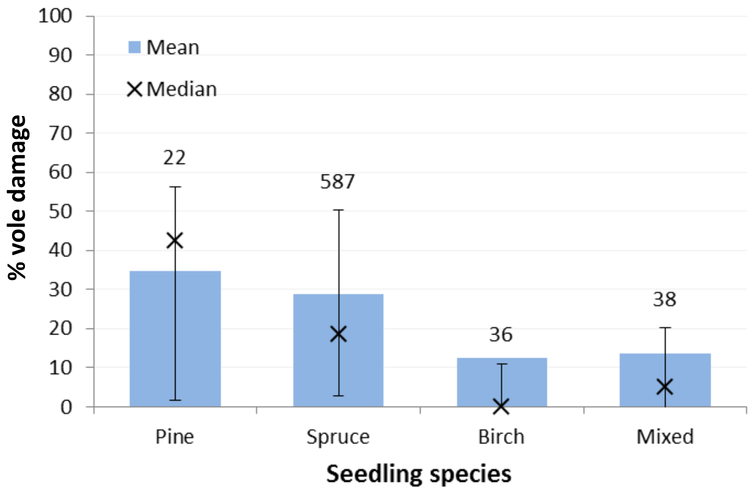

Figure 4. *Winter 2008/09 vole damage to planted seedlings in Päijät-Häme, categorized by leading healthy seedling species. Single-species stands are dominated (over 75% of living seedlings) by either pine, spruce, or birch, whereas "mixed" stands are stands where a single species accounted for 75% or less of the total number of healthy seedlings.*

The high level of pine damage is consistent with the study hypothesis and prior literature, but the relatively low level of birch damage is contrary to prior expectations. Teivainen (1979, Abstract) found that, generalized across all survey areas in Finland, 64% of the pine, 30% of the birch, and 6% of the spruce were damaged during 1973–1976. Seppänen (2010, 24) noted that seedling damage followed a similar species preference pattern (pine > birch > spruce); however, species differences were much smaller, and the relative damage of spruce much greater, than recorded in Teivainen (1979), although results cannot be directly compared due to Seppänen's inclusion of weevil and moose damage in his damage survey assessment. In contrast, Laitinen, Rousi, Tahvanainen, Henttonen, and Heinonen (2004, 2236) noted that field voles generally caused very low damage to birch seedlings in a trial examining the relationship between vole and hare damages and birch seedling species, fertilization, and age. Additionally, a survey of 2005/06 winter vole damage results from Finnish FMA seedling inspections found that the vast majority (82%) of vole damage occurred on spruce, 11% on pine, and only 7% on birch and other species (Huitu et al.

2009). It is not clear, however, whether this surprisingly high amount of spruce damage was a function of species preference or species availability.

Indeed, interspecific differences in vole damage likely result, at least in part, from the relative abundance of each seedling species in areas of highest vole density. During the 1970s when Teivainen (1979) examined species differences, pine was the regeneration species of choice; in contrast, more recent findings of relatively high spruce damage (Huitu et al. 2009, Seppänen 2010) may reflect the recent switch to planting more spruce (Ylitalo 2010, 128–129). The vast majority (86%) of stands in my survey data were spruce-leading, and given the record high vole population, it is plausible that voles ate whatever seedling species was available.

Additionally, in my study apparent species differences may be driven, in part, by differences in average seedling height between species. For pine-leading stands, mean/median seedling height was 70/35 cm, for spruce-leading 45/40 cm, for birch-leading 165/160 cm, and for mixed stands 60/40 cm. As already discussed, vole damage appears strongly related to seedling height; therefore, these findings of much higher spruce than birch damage are consistent with the height v. damage hypothesis.

Furthermore, Teivainen (1979, 10) notes that the relative proportion of species damage varies with type of regeneration area. In his study, clear cut regeneration areas had relatively more pine and spruce and relatively less birch damage than afforested field; indeed, 95% of the recorded birch damage occurred on fields (10). Because the majority of my study sites occurred in forest rather than field environments, it stands to reason that the damage to spruce would be higher, and birch lower, than results found by Teivainen (1979).

3.1.3 Seedling density

Using the t-test method of determining significance, there is no significant correlation between vole damage and total (damaged + healthy) surveyed seedling density (Spearman rank correlation, $p > 0.05$) (Figure 5). However, the

F-test method (refer to Methods and Materials, page 24) did give a significant result (Spearman rank correlation: r_s = -0.126, df = 681, p < 0.001). Regardless of the significance level, the correlation value is low due to the lack of a clear relationship. Therefore, it could be suggested that relative vole damage may decrease with increasing seedling density, but further research would be needed to confirm this observation. As Teivainen (1979, 18) noted, the distribution of damage is not solely dependent on the number of planted seedlings; instead, different regions, planting areas, and seedling species are more or less susceptible to vole damage. Therefore, seedling density is a poor indicator of vole damage and must be considered in combination with other seedling and site factors. Also, survey results only include natural seedlings if they were healthy and well-spaced; because vole-damaged natural seedlings were not included, surveyed densities cannot be strictly interpreted as total seedling densities.

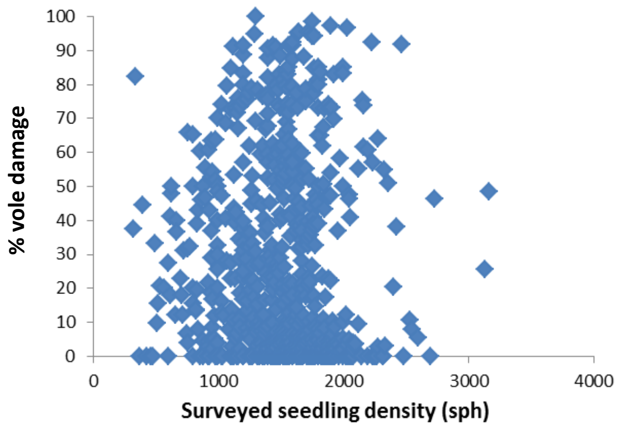

Figure 5. *Winter 2008/09 vole damage to planted seedlings in Päijät-Häme, as a function of seedling density (sph) per stand (n = 683). Seedling density combines all counted seedlings (i.e. both damaged and healthy planted seedlings, as well as healthy, well-spaced naturally regenerated seedlings) from the survey results.*

3.1.4 Seedling origin

Vole damage to planted seedlings was significantly lower in stands where healthy natural regeneration was present (Mann-Whitney U: U = 40508, z = -6.252, p < 0.001) (Figure 6.a). Additionally, in stands where healthy natural regeneration is present (i.e. bars to the right of the 0% bar in Figure 6.b), vole damage to planted seedlings appears to increase as the relative proportion of healthy natural regeneration seedlings increases.[4]

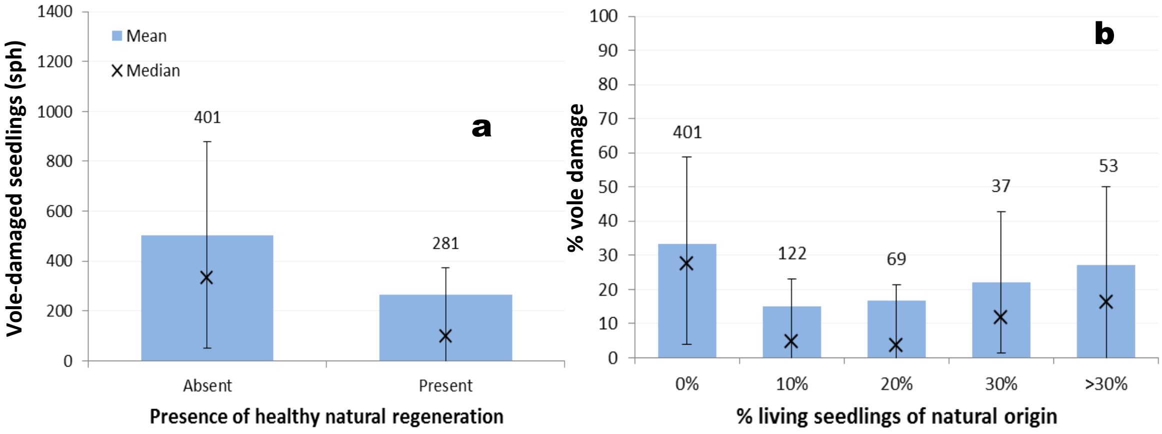

Figure 6. *Winter 2008/09 vole damage to planted seedlings in Päijät-Häme, characterized by a) presence/absence of natural regeneration and b) relative contribution of natural regeneration to healthy seedling stand (percentages on x-axis indicate upper bin limits, i.e. 0%, 0.1–10.0%, 10.1–20.0%, 20.1–30.0%, 30.1–100%).*

The finding of lower vole damage in stands where healthy regeneration was present is consistent with the study hypothesis. Vole seedling preferences may be influenced by seedling chemical composition, with greater avoidance of seedlings having higher phenolic [toxic defense] compounds (Roy & Bergeron 1990, Abstract). Some studies have shown a trade-off between positive seedling growing conditions (such as are found in greenhouse conditions) and the development of defensive compounds that hinder herbivory (Rodgers et al. 1993; Holopainen, Rikala, Kainulainen & Oksanen1995). Therefore, the lower vole damage observed among seedlings stands with healthy naturally regeneration may partially result from the buffering effect of natural regeneration's higher concentration of defense compounds.

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[4] For natural-regeneration presence/absence analysis (Figure 6.a), number of vole-damaged seedlings per hectare is used rather than percentage of vole damage; this was done because percentage vole damage is mathematically related to healthy seedling abundance (equation 2, page 20), making it difficult to distinguish biological significance from mathematical interdependence. By using number of vole-damaged seedlings, x and y axes are mathematically independent. This matter was solved in Figure 6.b by using the percentage of natural seedlings as a proportion of healthy natural seedlings to total healthy (natural + planted) seedlings, thus using relative rather than absolute seedling abundance.

Vole preference for planted rather than natural seedlings would also seem to be supported by Figure 6.b, where an increase in the relative abundance of healthy natural regeneration is associated with a corresponding increase in vole damage to *planted* (nursery-origin) seedlings. This seeming trend of "preferential browsing" on planted seedlings makes the important assumption that surveyed vole damage includes only planted seedlings (as stated in survey instructions). Due to the lack of data for natural regeneration vole damage, these results should be considered preliminary observations that require further investigation.

3.2 Vole damage as a function of site attributes

Summary: Compared to seedling factors, site attributes are relatively weak explanatory variables for vole damage. As an exception, however, vole damage appears to vary considerably with the dominate tree species prior to harvest. This relationship may arise from inherent site characteristics or from the impact of pre-harvest species on post-harvest regeneration.

3.2.1 Site classification

Contrary to expectations, vole damage on herb-rich heathlands (*lehtomainen kangas metsätyyppi*) was approximately 8% lower than on mesic heathlands (*tuore kangas metsätyyppi*) (Mann-Whitney U: $U = 9724$, $z = -2.256$, $0.01 < p > 0.05$) (Figure 7). Herb-rich heaths are grassy growing sites, whereas mesic heaths are characterized by abundant heath shrubs (notably bilberry, *Vaccinium myrtillus*) and ground moss, though grass may be rather abundant where forest-floor light levels are sufficiently high (Hotanen, Nousiainen, Mäkipää, Reinikaine & Tonteri 2008, 99, 115, 119). Due to the importance of herbaceous plants and grasses as food and shelter for voles, it was expected that the more abundant vegetation associated with the herb-rich forest type would result in correspondingly greater vole abundance and seedling damage in these sites. Indeed, Väkevä et al. (2010) suggests that the risk of vole damage to forest regeneration increases with site richness (*rehevyys*).

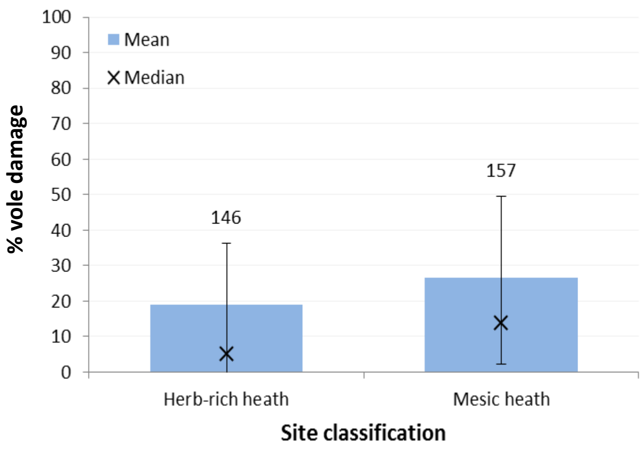

Figure 7. *Winter 2008/09 vole damage to planted seedlings in Päijät-Häme categorized by forest site type, where herb-rich heath corresponds to lehtomainen kangas and mesic heath to tuore kangas.*

Although contrary to my hypothesis, these results are similar to those of a recent study near Huittinen in southwestern Finland, where damage decreased and healthy seedling percentage increased with increasing forest-type richness (in decreasing order of percentage damaged: semi-dry heath *VT kuivahko kangas* > mesic heath *MT tuore kangas* > herb-rich heath *OMT lehtomainen kangas*) (Seppänen 2010, 25–26). Seppänen (2010, 42) attributes his similar findings partly to more effective weed control in the herb-rich sites.

In order to identify the underlying cause for this surprising finding in my own data, I examined whether the two forest types also differed in silvicultural treatment or seedling characteristics. Site preparation was practiced on over 90% of both forest types, and the site preparation methods (harrowing and scalping) with lowest vole damage were more commonly applied to the less rich (mesic) heath type. Therefore, differences in site preparation do not explain observed differences in vole damage between forest types. Furthermore, I found no difference between heath types in the relative abundance of natural seedlings (mean of 6.2 and 5.9% of healthy seedlings for herb-rich and mesic heathlands, respectively), total surveyed seedling density (mean of 1497 and 1504 sph, respectively), nor percentage of recently planted (2007–2008) stands (mean of 58% and 55% of stands, respectively). However, seedling species composition varied slightly between heath types, with more birch-dominated and no pine-dominated stands in the herb-rich heaths (birch was the most abundant healthy seedling species in 11% of herb-rich heaths and 4% of mesic heaths).

The finding of lower vole damage on the richer heaths may be due to differences in seedling species, local differences in vole abundance, or variables such as post-planting vegetation control that were not included in survey data. It is also possible that habitat preference assumptions weaken in the face of extremely high vole densities, when voles are forced to seek food even in non-favourable environments. Additionally, it may be necessary to account for a wider range of site description factors (understory vegetation species and ground cover, crown closure, etc.) in assessing forest site differences. Finally, the relatively small difference in vole damage between the two forest site types, and the fact that only two rather similar site types were included in this analysis, would caution against over-interpretation of these findings. These tentative observations should be confirmed with further research that specifically controls for a broader range of forest site types and includes a greater number of site-level descriptors.

3.2.2 Soil texture classification

Mean vole damage was slightly higher on coarse-textured and stony sites than on fine-textured sites, but this difference disappears when comparing median values (Figure 8). As would be expected, finer soil classifications were more common on herb-rich heaths than mesic heaths (27% and 9% of heaths, respectively), and it therefore follows that the lower levels of damage seen in herb-rich heaths would also be reflected in finer soils, though this finding may be unrelated to actual soil properties. The slightly higher vole damage observed on stony sites may be due to greater seedling susceptibility under more stressful growing conditions. Additionally, site preparation is more difficult to complete on very stony sties (Luoranen, Saksa, Finér & Tamminen 2007, 18), raising the possibility that vegetation was allowed to grow less hindered on these sites. Finally, according to Hansson 1994 (cited in Hansson 2002, 28), bank voles prefer shrublands and dense forests with abundant boulders. Therefore, it is possible that bank vole damage was higher in these stony areas. It is important to note that these are only speculations, however, and should be interpreted with caution given the small differences in damage between different soil types. Higher damage on peatland sites cannot truly be compared with other soil classifications due to the very small sampling size (n = 6).

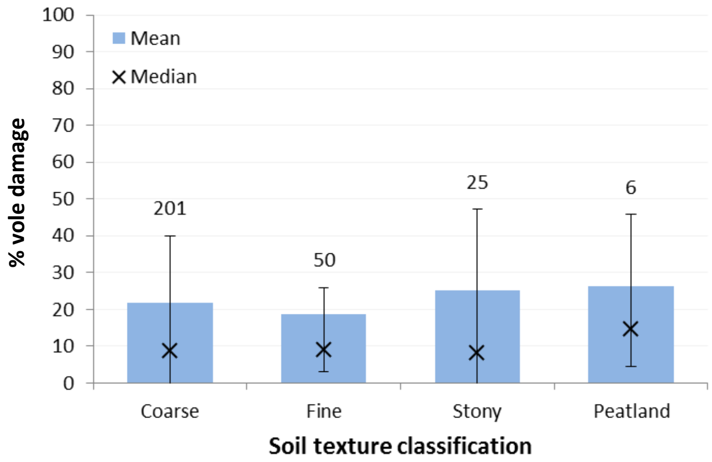

Figure 8*. Winter 2008/09 vole damage to planted seedlings in Päijät-Häme, categorized by soil texture classification. Soil texture classified according to SOLMU codes (SOLMU–peruskoodit 2009): coarse = keskikarkea tai karkea kangasmaa (class 10); fine = hienojakoinen kangasmaa, hienoainesmoreeni, and hienojakoinen lajittunut maalaji (classes 20, 21, and 22); stony = kivinen keskikarkea tai karkea kangasmaa (class 30); and peatland = turvemaa (class 60).*

3.2.3 Pre-harvest dominate tree species and age

The majority of pre-harvest stands (n = 251) were spruce-dominated (*Picea abies*), and seedlings regenerated in these stands also appear to have lower vole damage than in stands previously dominated by pine (*Pinus sylvestris*) (n = 25) (Figure 9.a). Only nine stands were identified as birch-dominated (*Betula pendula*) prior to harvest, and seedlings regenerated into these stands appear to have the highest mortality levels (Figure 9.a). There is no correlation between vole damage and pre-harvest forest age (Spearman rank correlation, $p > 0.05$), although stands with pre-harvest forest age below 30 years were excluded from this analysis (Figure 9.b).

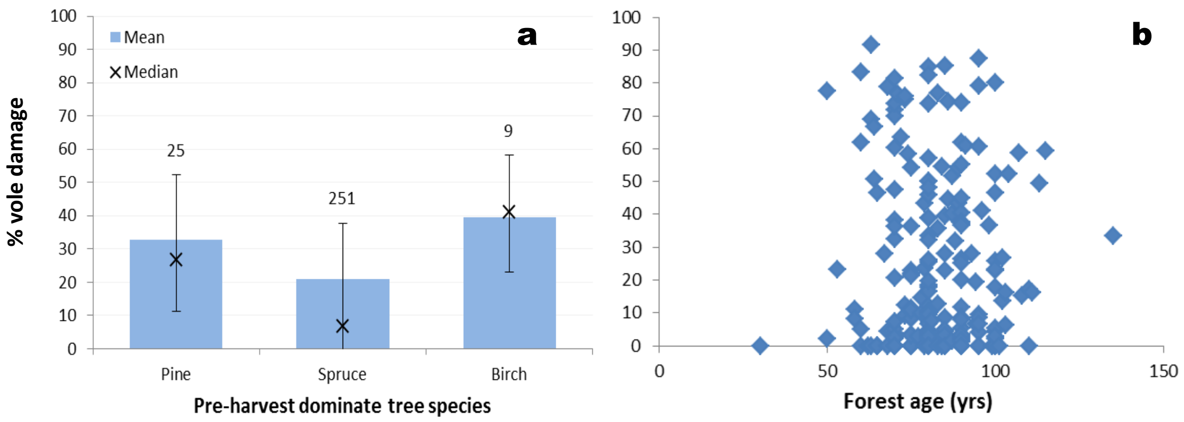

Figure 9. *Winter 2008/09 vole damage to planted seedlings in Päijät-Häme, categorized by a) dominant tree species and b) forest age prior to regeneration.*

Damage varied notably between sites dominated by different pre-harvest tree species. Mean vole damage was nearly 20% higher, and median damage 35% higher, on stands previously dominated by birch than on stands previously dominated by spruce. Birch could be expected to dominate on well-drained, nutrient rich sites—conditions which also favour abundant herbaceous vegetation. In addition, grass growth is highly sensitive to light conditions, growing much better in well-lit environments and forest openings than in shaded environments. Because both light and nutrient levels would be expected to be higher in birch- than conifer-dominated forests, it is not surprising that vole damage was also higher in these stands. In contrast, the dense canopy closure associated with spruce forests provides an unfavourable environment for grasses. Similarly, pine forests are typically more open, with higher understory light levels than spruce but fewer nutrients than deciduous stands; this explanation fits well with the finding of intermediate damage levels in previously pine-dominated stands. Indeed, dominate species may be a more useful indicator than forest type in explaining vole damage. Finally, the pre-existing forest structure affects naturally-regenerated seedling species and density.

The lack of correlation between forest age and vole damage is not surprising because a) forest age should be considered an estimate rather than absolute value; b) the range of ages studied is narrow, with nearly all stands between 50–100 years; and c) this study was not specifically designed to examine forest age, so the combining of all sites and species types into a single correlation analysis may obliterate any true correlation that would exist if only age were controlled for.

3.2.4 Stand surface area

These results show no clear relationship between seedling stand (or stand cluster) size and extent of vole damage (Spearman rank correlation, $p > 0.05$) (Figure 10). This is contrary to the findings of Hansson (2002, 31) that field vole damage was positively related to size of the reforestation area. However, vole species differences are evident in habitat selection. Unlike field voles, bank voles are a habitat generalist species preferring dense forest and shrubland (Hansson 1994 cited in Hansson 2002, 28). For these voles, proximity to forest edge may be an important factor (Hansson 2002, 31–32). Thus, as opening size increases, field voles could be expected to diminish while bank voles could increase, and the net effect on seedling damage may be difficult to predict. Furthermore, opening size alone is an insufficient determiner of seedling damage, because landscape-level factors (e.g. adjacency of other openings) also affect field vole damage (Hansson 2002, 31–32). The present study does not include information about tree age and structure in adjacent stands. Furthermore, the stand surface area variable in this survey data is more correctly an estimate of survey area. Most often individual stands were surveyed and analysed as a single, complete unit, but in some cases stand surface area represents area for a stand cluster or for smaller portion of a stand. Therefore, in future studies examining opening size, stand area needs to be defined more precisely and forest structure in adjacent stands must be taken into account.

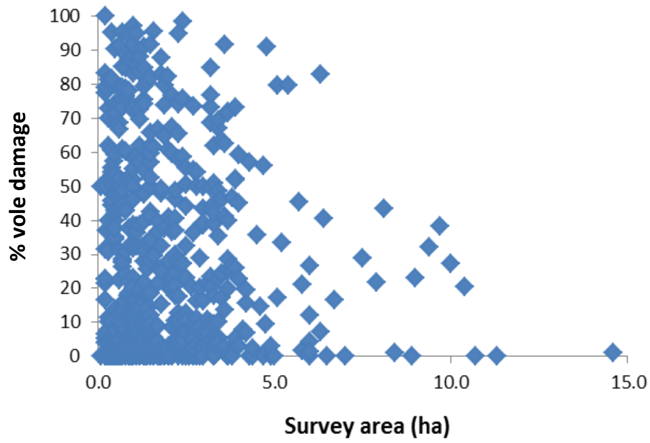

Figure 10. *Winter 2008/09 vole damage to planted seedlings in Päijät-Häme as a function of stand / stand-cluster surface area (n = 626).*

3.3 Vole damage as a function of silvicultural practices

Summary: It appears possible to manipulate vole damage using silvicultural techniques. Both site preparation and planting season appear to influence vole damage. These findings underscore the importance of management approaches that minimize herbaceous vegetation and maximize seedling growth potential.

3.3.1 Site preparation method

Vole damage appears lowest on stands prepared by harrowing (*äestys*, also known as disc-trenching) and scalping (*laikutus*) (Figure 11). Unprepared stands appear to have the highest vole damage among classified stands. "Unclassified" values (i.e. stands for which site preparation information is blank) have also been included in the visual analysis because it is assumed that at least a portion of these represent non-prepared stands, but due to the uncertainty these cases cannot be included in the "non-prepared" category.

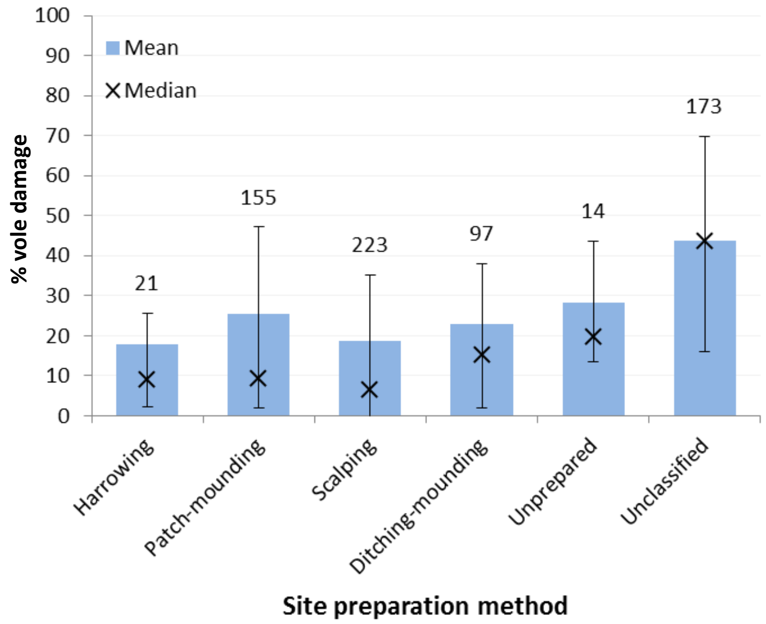

Figure 11. *Winter 2008/09 vole damage to planted seedlings in Päijät-Häme categorized by site preparation method: harrowing (äestys), patch-mounding (laikkumätästys), scalping (laikutus), ditching-mounding ([ojitus]mätästys), and unprepared (muokkamaton). "Unclassified" category includes stands for which site preparation was not recorded.*

The finding that site preparation decreases vole damage is consistent with my hypothesis and with prior literature. As found by Seppänen (2010, 39), the stronger the form of site preparation, the less vole damage present. In decreasing order of disturbed soil surface area, site preparation methods could be ranked harrowing, patch-mounding, ditching-mounding, and scalping and mounding (kääntömätästys) (Luoranen et al. 2007, 24). It is therefore consistent with expectations that lowest vole damage was found on stands prepared by harrowing (mean = 18% damaged seedlings). In contrast, non-prepared sites had a mean of 28% vole damage; that value increases to 44% if sites with no site preparation method recorded are included in the calculation. These findings underscore the importance of soil disturbance in reducing vole damage.

The mean vole damage percentage for patch-mounding treatment is surprisingly high (25%). However, this is partly explained by the right-skewed data distribution (note length of upper error bar in Figure 11). When considering median values, patch-mounding damage was only approximately 9% (Figure 11), which is consistent with the pattern that would be expected based on the amount of soil disturbance.

Contrary to my findings, Seppänen (2010, 26–27) observed lower vole damage in mounding than scalping treatments, although his observed differences and sample sizes were small (n = 17 for each). Indeed, according to the severity of site preparation treatment, it would be expected that ditch-mounded sites would limit vegetation (and as a consequence, vole damage) more effectively. However scalping is generally practiced on drier sites and ditching-mounding on wetter sites (also in this study scalping was more common on the drier heath type). When the site factor is taken into consideration, it seems possible that the greater surface area disturbance by the ditching-mounding site treatment may have been counter-balanced by more luxuriant vegetation growth on the wetter, richer sites. In future studies, the effectiveness of site preparation treatments could be assessed more effectively by controlling for the site richness factor and measuring vegetation cover before and after site preparation treatment. Also, it should be noted that these analyses primarily utilize surveyor information on site preparation method,[5] as surveyor information was often more stand-specific than FMA data. However, differences were often observed between site preparation as recorded by the field surveyor *versus* that recorded in the FMA database; therefore, differences in vole damage between site preparation methods must be interpreted with caution.

3.3.2 Time between site preparation and planting

Prior to expectations, there is no significant correlation between vole damage and planting delay (Spearman rank correlation, $p > 0.05$) (Figure 12). Any negative planting delays (i.e. site preparation after planting) were rejected in this analysis. Best forest management practices recommend planting soon after site preparation: site preparation should be conducted in the same year as planting, or, alternatively, in the previous fall (Luoranen et al. 2007). This helps to ensure that the benefits of site preparation are realized and seedlings have become well established prior to severe competition from regrowth of competing vegetation.

[5] FMA site preparation data was only used in cases where no method was recorded by the surveyor.

My finding of no correlation between planting delay and vole damage could be due to the uncertainty in estimated dates. Planting delay was extrapolated based on data available in the FMA database, but these extrapolations may not be correct. In particular, in many cases seedling order date was used as a surrogate for planting date if more precise data were not available. However, this assumption may be not be accurate if seedlings were ordered many weeks prior to planting, or if billing was processed long after planting.

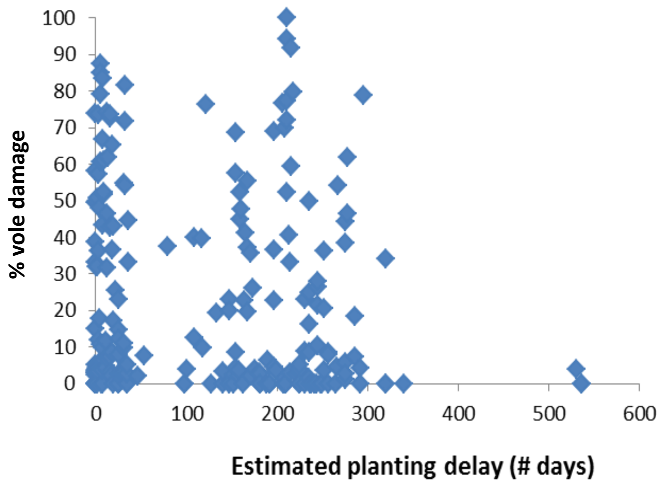

Figure 12. *Winter 2008/09 vole damage to planted seedlings in Päijät-Häme as a function of estimated time lag (number of days) between site preparation and planting (n = 228).*

3.3.3 Planting season

Although sample sizes are highly uneven (n_{spring} = 256, n_{fall} = 32), it appears that seedlings planted in fall (September-October) suffered greater vole damage than seedlings planted in spring (prior to July 1) (Mann-Whitney U: U = 3158.5, z = -2.111, $0.01 < p > 0.05$) (Figure 13). The finding of greater vole damage on fall-planted seedlings is consistent with expectations. Because the majority of vole damage occurs during winter, at least for coniferous seedlings (Henttonen 2001, 285), and because seedling size is strongly related to vole damage, it follows that seedling size at the beginning of the winter should be of greatest importance. Seedlings planted in spring have already had one growing season in the field by the time winter approaches, whereas fall-planted seedlings have not. This addition of one growing season in the field may not only be important for increasing seedling size, but also harsher field environments may strengthen seedlings' defense ability and toxic bark compounds, making them both more resistant and less tasty to voles. According to Finnish vole researcher Heikki Henttonen, fall-planted seedlings have received nitrogen additions at the nursery during the summer and therefore taste better than other seedlings to voles (quoted in Palokallio 2011b). Findings in this study must be interpreted with caution, however, as the majority of fall-planted seedlings were planted in 2007 and 2008, whereas spring-planted seedling planting dates ranged from 2004–2008. As previously shown (Figure 3.b), seedlings planted prior to 2007 had much lower vole damage.

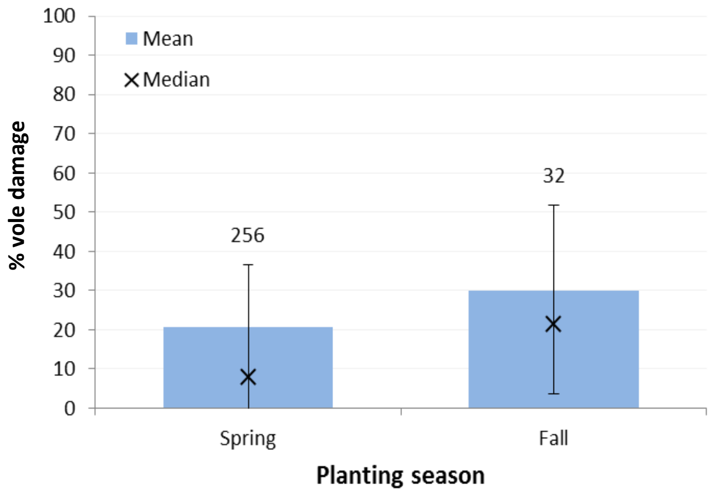

Figure 13. *Winter 2008/09 vole damage to planted seedlings in Päijät-Häme categorized by planting season (spring = planting prior to July 1, fall = planting in September–October).*

3.3.4 Planting density

There is no correlation between vole damage and estimated planting density[6] (Spearman rank correlation, $p > 0.05$) (Figure 14). As shown on the right-hand side of Figure 14, three apparent outliers (density = 4020 sph x 2, 5040 sph) have

[6] calculated by dividing seedlings ordered or planted by stand area (ha).

been included in the correlation; however, eliminating them from the analysis only weakens the correlation values. This finding of no relationship is similar to that already discussed in regard to survey seedling densities (section 3.1.3). In addition, planting densities are estimated only and must be interpreted with caution. In many cases, data in the FMA database included seedling quantities for several stands combined, in which case stand density was estimated by dividing total seedling number by the sum of stand surface areas. It should also be noted that stand surface areas in the FMA database often differed from those recorded by the field surveyor, increasing uncertainty as to the reliability of planting density estimates.

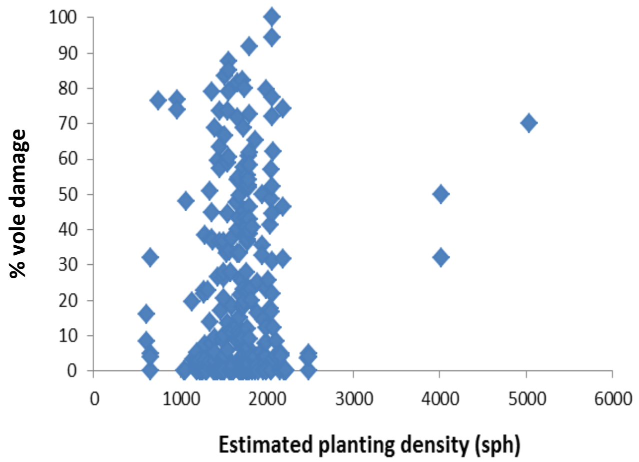

Figure 14. *Winter 2008/09 vole damage to planted seedlings in Päijät-Häme as a function of estimated planting density (sph) (n = 274). Planting density calculated from FMA data by dividing number of seedlings ordered or planted by stand surface area.*

4 CONCLUSIONS AND RECOMMENDATIONS

4.1 Primary significance of the study

This study succeeded in identifying seedling, site, and silvicultural factors underlying record high levels of vole damage to seedlings during winter 2008/09. In particular, the large geographical scale, broad range of factors examined, and large sample sizes strengthen observed trends and provide an unusually comprehensive contribution to previous vole damage research. Furthermore, the use of data from ordinary forestry survey methods and the standard Forest Management Association database provide a useful example of how research can be integrated with normal forest management procedures to provide data and methods readily available and practically applicable at a broad scale. Finally, the exceptionally high vole damage during winter 2008/09 provided a unique opportunity to assess seedling damage under extreme conditions—conditions which may become increasingly common if current vole population fluctuation trends continue (Huitu et al. 2009, 1223).

The most important findings of this study are the relationships between vole damage and a) seedling size, b) seedling species, and c) site preparation. Additionally, this study provided some noteworthy insights on the relation between vole damage and natural regeneration, planting season, and pre-harvest forest attributes.

First, these results confirmed the importance of seedlings size: in all variables studied (height, year of planting, and planting season), highest levels of vole damage occurred on smaller and/or younger seedling stands. In particular, there was a clear decrease in seedling damage for seedlings exceeding 50 cm height and for seedlings with at least 3 field seasons. Above these thresholds, mean vole damage was near or below 10% of the seedlings—levels which probably would not jeopardize the overall health of a stand planted to full density. This height threshold is lower than that suggested by prior literature (Teivianen 1979, 7, 10).

Second, this study confirmed the susceptibility of pine to vole damage. Despite similar median height for pine and spruce, both mean and median vole damage on pine-dominated seedlings stands appears higher than for spruce. However, it is important to note the large difference in sample sizes.

Third, these results confirm the usefulness of site preparation for reducing vole damage. Importantly, this study covered four commonly-used site preparation methods as well as the option of no site preparation. Of the options used, harrowing and scalping provided the best results, although all site preparation treatments were better than no site preparation. It is not fully clear from this study whether differences in vole damage between site preparation treatments are due to different methods being used on different *site types* (where site conditions favourable to grass growth could also lead to greater vole abundance despite more intensive site preparation), or whether this finding is related to differences between site preparation methods in the *extent of soil disturbance*. Additionally, differences must be interpreted with caution due to possible inaccuracies and variation between surveyors in recording site preparation method.

4.2 Applications

Seedling establishment is the most critical phase of forest management. Without a healthy, vigorous growing stock, efforts to achieve a productive forest become both futile and expensive. Conversely, investing in best management practices at the replanting and seedling establishment phases can reduce the need for and cost of subsequent stand improvement practices, as well as providing a faster rotation time and higher return on investment. Because vole damage is one of the critical factors threatening successful seedling establishment in areas of Finland, measures to reduce seedling susceptibility to voles and to increase seedling vigour must be implemented. Based on the results of this study as well as prior research, forest managers can take several clear steps toward this aim.

First, some form of site preparation is important for reducing the detrimental effects of voles on seedlings stands. This finding is not new (see recommendations in Raulo 1978, 18–19, 22; Henttonen 2001, 286; Väkevä et al.

2010), but has been strongly re-enforced by results from this study. Tentative observations suggest that methods such as harrowing which disturb a larger percentage of the soil may be most effective. However, the optimal form of site preparation must be made at the stand level taking into account local drainage and soil factors as well as visual quality objectives. Numerous guides, such as *Metsämaan muokkausopas* (Luoranen et al. 2007 *in Finnish*), are available to assist with this decision.

Second, the timing of reforestation is important. When possible, replantings should be timed for the spring following the collapse of the vole cycle (Teivainen 1979, 21). This is done to provide at least two seasons of growth during low vole abundance, thus maximizing the possibility for seedlings to reach the 50 cm height threshold prior to the next vole population peak. Tentative results from this study would also indicate that in areas of known susceptibility to vole damage, spring planting should be conducted in favour of fall planting. This may be particularly true for conifers in reforestation areas, which are consumed almost exclusively during the winter months and therefore benefit from the addition of one growing season prior to the onset of winter.

Third, planting at higher densities and encouraging natural regeneration could help decrease the need for fill-planting in the event of vole damage. Relative vole damage did not increase with increasing planting densities nor total seedling densities. Furthermore, planted seedling damage was significantly lower on stands with healthy natural regeneration. Therefore, higher-density planting and natural seedling recruitment could help ensure sufficient stocking even after vole damage has occurred. Natural regeneration can be encouraged through site preparation and the use of seed trees, for example, although sole reliance on natural regeneration may not be recommendable due to smaller initial seedling size and the risk of insufficient stocking density.

Fourth, pure pine seedling stands should be avoided in vole risk-prone areas. Pine is not only damaged more frequently than spruce, but it also develops stem deformities more easily following leader removal by voles (Henttonen 2001, 288). Even on sites where pine is the most suitable species, it may be advisable to plant a species mix rather than pure pine monoculture. However, species selection alone is insufficient protection from vole damage, as results from this study show that spruce is also highly susceptible in peak vole population conditions.

Finally, forest managers must consider underlying site conditions and pre-harvest forest factors. In particular, grassy areas dominated by birch prior to harvest may be at high risk to vole damage, whereas dense spruce forests may be lower risk areas for replanting. High-risk areas may require more expensive vegetation control measures (including site preparation and herbicide or other weed control) as well as direct seedling protection from voles (using seedling guards and vole poison, for example) in order to establish a healthy seedling stand. Henttonen (2001) provides a useful overview of seedling protection alternatives. Forest owners would do well to consider the cost and time of seedling establishment and protection before making the decision to log these high-risk stands.

4.3 Study limitations and suggestions for further research

The very benefits of this study also bring drawbacks: using broad, forestry-management survey results leads to less precision and difficulty in detecting factors important at the small scale. For example, the large number of field surveyors enables the collection of much more data than would typically be possible in conventional research, but it also introduces variability into survey procedures and data. Futhermore, the record high vole population levels may have led to unusual feeding behaviour, partly explaining the lack of relationship between forest site type, seedlings density, etc.. Additionally, the general lack of clear or easily explainable results in comparing site factors with vole damage could be due to the fact that only two rather similar forest types were analyzed. Including a broader range of sites from dry heath (*kuiva kangas*) to grove (*lehto*) and controlling for similar forest management practices across all sites could result in clearer results. Finally, the effect of environment (field *v.* forest) is also important when comparing with past literature. As previously mentioned, this could provide one explanation for why birch damage was so surprisingly low, and spruce so surprisingly high in my study compared to Teivainen (1979).

As with all short-term research projects, this data is only a snapshot. It is important to remember that in reality, vole abundance and vole damage is cyclical. The relative importance of various factors may vary in any given year or in any given location with vole abundance and site attributes. Indeed, Teivainen (1979) mentions different patterns (e.g. species preference) in different years. Further research should focus on following key variables identified in this study over a longer period of time, at least one entire vole cycle.

This study revealed some important tentative findings that require further research and verification. In particular, the relative susceptibility of planted versus natural seedlings to vole damage is well worth further research. As concluded by Puukila (2010, 31), understanding differences between the palatability of different seedlings and developing seedlings non-desirable to voles are important areas of future vole damage-prevention research. If naturally regenerated seedlings are less desirable to voles, they could provide a low-cost alternative to minimizing vole damage. Second, further research should confirm the greater resistance of spring- versus fall-planted seedlings as tentatively observed in this study (also mentioned in Palokallio 2011b). Such research would be easy to conduct, and if a significant impact is found, spring-planting is easily integrated into planting recommendations and implemented in the field, thus providing a simple means of reducing vole damage. Third, given the importance of seedling size as found in this study and confirmed by prior research, further studies should compare vole damage among different planting stock sizes planted within the same year. For example, a study could be conducted comparing *pikkupaakku 1v*, *keskipaakku 2v*, and *isopakku 2v* containerized spruce seedlings. Finally, weed control (*heinäntorjunta*) was not directly studied in this thesis but may have influenced the finding of lower vole damage in the fresher site type (Seppänen 2010, 42). Further studies should also account for different intensities in weed control and its ability to decrease vole damage. Given the high cost of vole damage to forest owners as well as state support systems (e.g. Kemera funding in Finland), it is important that further vole damage research be conducted in close connection with forest managers to develop practically applicable methods of reducing vole damage in seedlings stands.

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Table A5.07: Critical values for the Wilcoxon/Mann-Whitney Test (U). 2011. [Online document]. Alamo Colleges, *Puentes* Partnership, San Antonio College (Texas). [Ref. 30 April 2011]. Available at: http://www.alamo.edu/sac/media/ puentes/Documentation/CriticalValuesU.pdf.

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APPENDICES

APPENDIX 1. Municipality-level summary of data retained for analysis.

Municipality	Percentage of original data included in analysis	Number of stands	Mean percentage vole damage
Asikkala	85%	190	38%
Hartola	0%	0	-
Heinola	90%	84	51%
Hollola	75%	43	7%
Hämeenkoski	95%	33	6%
Kärkölä	90%	107	4%
Nastola	0%	0	-
Padasjoki	85%	70	33%
Sysmä	85%	147	24%
Other	75%	9	39%
TOTAL	***65%***	***683***	***27%***

APPENDIX 2. Summary of field inventory and Forest Management Association database variables for summer 2009 vole-damage surveys.

	Description	Data-source
Property data		
Municipality *Kunta*	Official municipality in which the stand is located	Field notes, site maps
Village *Kylä*	Village/town near which the stand is located	Field notes
Property *Tila*	Forest property name	Field notes
Owner *Omistaja*	Forest owner name	Field notes
Observer *Inventoija*	Name of trainee who surveyed the given stand	Field notes
Responsible forester *Vastuualue*	Responsible forester for the given stand	Field notes
Forest plan number *Metsäsuunnitelma numero*	Forest plan identification number for the given stand	Field notes, site maps
Site plan number *Työmaa numero*	Site plan identification number for the given stand	Field notes, site maps
Stand number *Kuvio*	Stand number(s) according to the forest plan.	Field notes
Stand ID *Kuvio ID*	Unique stand identification number used in analysis. Most often individual stands were surveyed, numbered, and analysed as a single, complete unit. However, in cases where *several* stands were simultaneously surveyed as a single stand cluster, these were assigned a single stand ID and analysed as a single unit. In cases where a stand was *divided* into two or more distinct survey areas, each was assigned an individual stand ID. ** In this report, "stand" refers to the stand, stand cluster, or stand portion having a unique stand ID number. All stand analyses conducted according to stand ID.*	Derived
Surface area *Pinta-ala*	Stand surface area (hectares) as recorded and surveyed by field surveyor. Surface area follows the same rules used for stand ID (above). FMA surface area values used if no value recorded by surveyor.	Field notes, site maps, FMA database

Survey variables

Survey date *Kenttätyö päivämäärä*	Date of summer 2009 survey	Field notes
Spring height *Pituus keväällä*	Average height (cm) for leading seedling species, only for stands measured prior to June 1, 2009.	Field notes
Height *Pituus*	Average height (cm) for leading seedling species, all stands irrespective of survey date.	Field notes
Planted pine/spruce/birch *Istutettu mänty/kuusi/koivu*	Mean number of healthy, planted seedlings (separate columns for pine, spruce, and birch) per hectare.	Derived from field notes
Natural pine/spruce/birch *Luontaiset mänty/kuusi/koivu*	Mean number of healthy, well-spaced, naturally regenerated seedlings (separate columns for pine, spruce, and birch) per hectare.	Derived from field notes
Damaged/dead seedlings *Kasvatuskelvottomat/Kuolleet taimet*	Mean number of vole-damaged/-killed planted seedlings (pine, spruce, and birch combined) per hectare. Seedling classified as vole-damaged/killed if bark stripped from more than 50% of the circumference. Seedlings chewed along the leader but retaining most recent year's growth considered healthy. Only winter 2008/09 vole damage recorded.	Derived from field notes
Total seedlings *Taimet yhteensä*	Sum of all recorded healthy (planted+natural) and damaged/ killed (*planted*) seedlings per hectare	Derived
% damaged/dead seedlings % kasvatuskelvottomat/ *kuolleet taimet*	Mean vole-damaged/-killed planted seedlings as percentage of total seedlings.	Derived
% living seedlings of natural origin *% luontaiset kasvatuskelpoisistataimista*	Derived by 100% (total healthy natural seedlings / total healthy natural + planted seedlings)	Derived
Seedling species *Taimien laji*	Seedling species characterization for healthy (planted + natural) seedlings: assigned a single species code if one species comprises >75% of the healthy seedlings; otherwise, double species code for the two most prominent species. Stands with a double species code termed "mixed" seedlings stands in the report.	Derived
Field comments *Huomioita*	Field surveyor comments on seedling condition, site characteristics, etc.	Field notes

Forest Management History

Harvest age *Metsän ikä hakkuussa*	Approximate forest age at time of harvest.	FMA database
Harvest species *Pääpuulaji*	Leading tree species.	FMA database
Harvest method *Hakkuutapa*	Harvest method (clearcut, shelterwood removal, etc.). Harvest method is clearcut (*avohakku)* in nearly all cases with data.	FMA database
Harvest year *Hakkuuvuosi*	Year and estimated month of harvest, generally based on FMA *valtakirjakauppa* date.	FMA database,
Clearing date *Raivaus päivämäärä*	Approximate clearing date. Not used in this analysis	FMA database
Regeneration date *Uudistamispäivämäärä*	Regeneration date (estimate) and year. For planted stands, seedling order date was often used as a surrogate for planting date if exact planting date was not available. FMA regeneration dates used instead of surveyor-recorded regeneration year estimates.	FMA database
Planting season *Istutusaika*	Spring (prior to July) or Fall (September–October).	Derived from FMA database
Planting density *Istutustiheys*	Calculated planting density *estimate* (sph) obtained by dividing seedling amount by FMA planting surface area.	Derived from FMA database
Seedling type *Taimet*	Seedling species, age, and containerized/ bare-root information.	FMA database
Seedling stock number *Mv-mat. erätunnus*	Identification number for seedling stock.	FMA database
Site preparation date *Maanmuokkaus päivämäärä*	Approximate site preparation date.	FMA database
Site preparation *Maanmuokkaustapa*	Site preparation method as recorded by field surveyor. Methods include harrowing *äestys*, patch-mounding *laikkumätästys*, scalping *laikutus*, mounding [*ojitus*]*mätästys*, unprepared *muokkamaton*, and unclassified (information left blank). FMA data used if no method recorded by surveyor.	Field notes, FMA database
Planting delay *Istutus viivästys*	Calculated number of days between site preparation and planting. Used in analysis if site preparation date no later than planting date.	Derived

Site characteristics

Ecosystem subgroup *Alaryhmä*	Heath or mire designation, according to standard forestry classification	FMA database
Site class *Kasvupaikka*	Site type, according to standard forestry classification	FMA database
Soil class *Maalaji*	Soil/peat type, according to standard forestry classification	FMA database
Inventory year *Inventointi vuosi*	Forest inventory year	FMA database